

CHROMOSOME NUMBERS AND GEOGRAPHIC
DISTRIBUTION IN *CHAENACTIS DOUGLASII*
(COMPOSITAE, HELENIEAE)

JOHN S. MOORING

Biology Department, Santa Clara University,
Santa Clara, CA 95053

ABSTRACT

A report of $2n=15$ II is new for *Chaenactis douglasii* (Hook.) Hook. & Arn., as are 12 II and 18 II for *C. douglasii* var. *montana* M. E. Jones. The frequency of meiotic aberrations (11%) was 33% of that found in a larger 1980 study. The correlation between ploidy level and age of substrate was highest in the Sierra Nevada and lowest in the Intermontane Plateaus.

Chaenactis douglasii (Hook.) Hook. & Arn. ranges from near sea level to over 3000 m from the Pacific Coast states to British Columbia, Montana, Wyoming, Colorado, and Arizona. These winter annuals, biennials, or short-lived perennials occur in dry and often disturbed sites in diverse soils and plant communities. Taxonomic treatments differ widely, from ten species and six varieties (Stockwell 1940) to one species and five varieties (Abrams and Ferris 1960). Gillet (1954), Alava (1959), and Raven and Kyhos (1961) reported chromosome counts of $2n=24$, $2n=12$, and $2n=12$, 24 and 36, respectively. In a study of 500+ plants Mooring (1965, 1980) reported triploids ($2n=18$) and many tetraploids and hexaploids with rings or chains of chromosomes, as well as diploids or polyploids with one or more extra, full-sized chromosomes.

The geographic distribution of diploid and polyploid populations was correlated with age of the substrate. Evidence suggested that the *C. douglasii* complex evolved in late Cenozoic time as major climatic and geologic changes induced migration and hybridization. Polyploidy stabilized the hybrid derivatives, and, tolerant of increasing aridity, they colonized newly available habitats in areas disturbed by volcanic activity and glacial or glacial-related processes (Mooring 1980).

The 1980 study rested on uneven geographic sampling. British Columbia, Wyoming, and Colorado were represented by a total of only ten populations, and few samples elsewhere came from mountains projecting above arid or geologically recent intermountain plateaus. Since then I have sporadically sampled more populations while traveling, and also have undertaken a hybridization program.

My purpose here is to describe the results of the additional sampling, especially in British Columbia, Wyoming, and Colorado.

METHODS

One count came from buds collected in the field, 14 from field plants transplanted to the greenhouse, and 20 from greenhouse or garden plants grown from field-collected fruits. Microsporocytes or, in four cases, root tips were squashed in acetocarmine, the former after fixation in 1:3 acetic ethanol, the latter after 6–8 minutes in concentrated HCl-95% ethanol (Mooring 1975). Meiotic studies were of cells during diakinesis or metaphase I; determinations rest on at least 12 clear cells. Root tip counts generally were of prophase stages and rest on 4–6 clear cells. Nine counts are not accompanied by voucher specimens because the plants died suddenly or were used in artificial hybridizations. Identities of the plants are certain. Information about the age of the substrates at population sites in the U.S. came from USDI Geological Survey maps, scaled at 1:500,000 for Colorado, Nevada, Oregon, and Washington, and at 1:750,000 for California. The scale for British Columbia was 1:1,267,200.

RESULTS AND DISCUSSION

Some populations of this complex do not fit nicely in one or another of the various varieties. If pressed, I would place all but two of the populations in this report in var. *achilleifolia* (Hook. & Arn.) A. Nels. The exceptions are populations 302 and 316, which are assignable to var. *montana* M. E. Jones.

Cytological aberrations were relatively infrequent (11%) in these samples (Table 1). In contrast, about 33% of the individuals studied previously (Mooring 1980) had multivalents, chromosomes in excess of the basic complement, an unusually large or an unusually small bivalent, secondary associations between bivalents, unpaired chromosomes, or a fragment chromosome. In the present study one tetraploid occasionally formed an association of 4 chromosomes, another had a fragment chromosome. In the 1980 study 50% of the tetraploids had multivalents, extra chromosomes, or both. The 300% difference in the frequency may be sampling error or attributable to greater diploidization of the tetraploids in this sample. At the diploid level one plant had an extra, full-sized chromosome and another had two, which generally paired. These chromosomes in excess of the basic complement will be referred to as supernumerary chromosomes.

The count of 15 bivalents seems to be a new report for this species, and those of 12 and 18 bivalents are new reports for var. *montana* (Table 1). Another member of that population had 12 II, and 13 II and 14 II counts have been obtained in other populations (Mooring 1980). Supernumerary (=B or accessory) chromosomes occur in many species. In some they can be transmitted through the maternal or

paternal line, and sometimes multiplied, as in the female line in *Clarkia unguiculata* (Mooring 1960). Stuessy (1990, p. 292) commented that *Chaenactis douglasii* has a great range of variation in number of chromosomes; the 15 II count adds to that range. The presence of one to six supernumerary chromosomes in *C. douglasii* individuals, and their presence in many populations (Mooring 1980) suggest that they persist for one or several reasons; they can be multiplied or at least transmitted, they have adaptive value, or they are not harmful enough to be eliminated by selection.

Mooring (1980) reported that diploids predominated in the Pacific and Rocky Mountain systems, and polyploids in the intermontane plateaus comprising the Columbia Plateau, Basin-and-Range, and Colorado Plateau provinces. After comparing soil, vegetation, altitude and what climatic data could be applied, it became apparent that a correlation existed between the ploidy level of populations and the age of underlying or nearby substrate (Mooring 1980). Generally, polyploid populations were on Quaternary or occasionally on Pliocene or Miocene substrates, whereas diploids were on soils derived from older rocks. Most polyploid populations occupied naturally disturbed regions—former glacial lakes (Montana), lands scoured by the Spokane Flood(s) (Washington), regions where the soils were derived from Quaternary or late Tertiary lava flows (eastern Washington and Oregon, southern Idaho, northeastern California, northern Sierra Nevada), or moraines (California). Diploid populations, on the other hand, were on older substrates undisturbed by volcanic and glacial or glacial-related forces. The ploidy level-substrate correlation was not 1:1. See Mooring (1980, pp. 1311–1314) for a more complete description.

The distribution pattern of the 14 diploid, 11 tetraploid, and two hexaploid populations in this study (Table 2) is consistent with that described (1980) for 68 diploid, 110 tetraploid, and 19 hexaploid populations. The degree of correlation between ploidy level and substrate age and disturbance varied regionally, as it did in the 1980 study. This time it was highest in the Sierra Nevada and lowest in the Intermontane Plateaus.

In the Sierra Nevada the correlation between diploid populations on soils derived from geologically older rocks and polyploids on younger ones was perfect: two diploids on Mesozoic granite and four tetraploids on Miocene volcanic material (Table 2).

In the Basin-and-Range Province portion of the Intermontane Plateaus two of the three California and Nevada diploid populations did not fit the diploid-old substrate hypothesis. Population 280, on soils derived from Pliocene or Pleistocene sedimentary rocks, is 16 km down Long Valley Creek from diploid population 208 and on the same substrate. Mooring (1980) noted that 208 was an ex-

TABLE 1. CHROMOSOME COUNTS AND MEIOTIC ASSOCIATIONS IN *Chaenactis douglasii*. Locations are approximate. The bolded 3-digit number immediately preceding a location is the population number; 4-digit numbers indicate my collection numbers. I collected all populations but 286 and 287. My voucher specimens have been deposited in SACL, those for 286 and 287 in CS. Numbers in parentheses indicate numbers of individuals counted, if more than one. An asterisk denotes the plant died before furnishing a herbarium specimen, and RT means root tip count.

Location	Chromosome count
California	
Alpine Co., 285 , Highland Lakes Road, *	2n=12 II
Fresno Co., 282 , Mono Creek, *	2n=6 II, 2n=11-12 (RT)
Mariposa Co., 278 , Sentinel Dome, Yosemite N. P. *	2n=6 II
Mono Co., 316 , Sonora Pass, 3653	2n=12 II
Sierra Co., 281 , Sierraville, 3474	2n=12 II
Lassen Co., 280 , Constantia, 3745	2n=6 II (2)
276 , SW flank, Skeeaddaddle Mt. 3473	2n=12 II
Nevada	
Eureka Co., 288 , 30 mi W of Eureka, 3547	2n=6 II 1 I
Nye Co., 283 , Grantsville, 3494	2n=6 II (2)
Oregon	
Sherman Co., 315 , Moro, 3700	2n=12 II
Colorado	
Archuleta Co., 290 , Arboles, 3528	2n=6 II (2)
Rio Blanco Co., 286 , T1S R100W S 28, Kelley & Waters 82-190 (CS)	2n=6 II, 2n=12 (RT)
287 , T2S R99W S 25, O'Kane & Sigstedt 82-425 (CS)	2n=12 II, 15 II
San Miguel Co., 289 , Norwood Hill, 3633	2n=12 II
Grand Co., 298 , Kremmling, 3548	2n=12 II
Gunnison Co., 295 , Monarch Pass, *	2n=6 II
293 , Powderhorn, *	2n=7 II
Hinsdale Co., 292 , Lake City, *	2n=6 II
Jackson Co., 300 , Walden, *	2n=12 II, 1 fragment
Pitkin Co., 297 , Thomasville, *	2n=6 II
Wyoming	
Teton Co., 277 , Gros Ventre R., Teton N. P., 3476	2n=18 II
Carbon Co., 302 , Lincoln Park, 3534	2n=18 II
Sweetwater Co., 305 , Point of Rocks, 3743,	2n=6 II, 2n=12 (RT)
British Columbia	
312 , Bear Creek Provincial Park, 3679	2n=6 II (2)
314 , Penticton, *	2n=12 (RT)
308 , Spence's Bridge, 3638	2n=12 II
309 , Princeton, 3675	2n=12 II

ception to the ploidy level-substrate age correlation. Population 288 was on Quaternary alluvium, but within 13 km of Cretaceous and older rocks on Antelope Peak (3144 m). Mooring (1980) described a similar situation for Nevada diploid populations 154 and 218.

The single Columbia Plateau population (315, tetraploid, on Pliocene gravels) fit the polyploid-young substrate hypothesis, but the two Colorado Plateau tetraploid populations (287, 289) did not (Table 2).

The ploidy level-substrate age correlation held in the Rocky Mountains. The four diploid populations were in soils underlain by Eocene to Precambrian igneous or volcanic rock, and the single hexaploid (277) was on Quaternary alluvium (Table 2). The two tetraploid populations (298 and 300) were on Cretaceous or Eocene substrates, but were in "parks," unforested basins in a syncline between mountain ranges (Fenneman 1931). The parks probably are geologically quite recent compared to the mountains that contribute their erosion products to these basins.

The Wyoming Basin populations are represented by a diploid (305) on a Cretaceous sandstone ridge between basins, and a seemingly out-of-place hexaploid (302) on a Precambrian substrate in the Carbon Basin. These and other Wyoming basins, like the Colorado "parks," probably are much younger than the surrounding mountains. The North Platte River (8 km from 302) drains the Carbon Basin and North Park, where population 300 (tetraploid) occurs (Table 2).

It was difficult to decide which substrates were present under the British Columbia populations because many substrates were present and the map scale was 1:1,267,200. The two diploid populations, on very dry and shallow-soiled sites under *Pinus ponderosa* and *Pseudotsuga menziesii*, appeared to be on Eocene or Precambrian sedimentary or metamorphic substrates. Tetraploid population 309, in sandy soil under the same conifers, appeared to be on Pleistocene glacial lake deposits. These three fit the ploidy level-substrate age hypothesis. Tetraploid population 308, in heavy clay soils derived from a Cretaceous sedimentary rock substrate, did not. It was along the Nicola River in an *Artemisia tridentata* community, however, probably a much more recent environment than conifer forest.

One would predict imperfect correlations in this study for the following reasons. First, it is sometimes difficult or impossible to locate precisely a population on a geological map where substrates of very different ages and kinds are jumbled together ("eggbeater geology"). Second, these maps may not identify small, geologically different sites speckling an extensive and monotonous surface. Third, highway building and other disturbances facilitate the establishment of *Chaenactis*. Fourth, the existence of polyploids in a diploid region may result from the fusion of unreduced gametes. (I regard the origin of diploids from tetraploids as considerably less likely.)

The correlation between ploidy level and substrate age and disturbance in *C. douglasii* might, of course, represent a correlation between ploidy level and climate, rather than ploidy level and geo-

TABLE 2. COMPARISON OF PLOIDY LEVEL, SUBSTRATE, SOIL, ELEVATION, AND PLANT COMMUNITY.

Popula- tion	Substrate	Soil	Eleva- tion (m)	Plant community
Sierra Nevada				
California				
diploid				
282	Mesozoic granite	sandy	2500	Jeffrey Pine Forest
278	Mesozoic granite	sandy	2000	Red Fir/Jeffrey Pine
tetraploid				
285	Miocene volcanics	clay	2500	Jeffrey Pine Forest
276	Miocene volcanics	clay	1500	Sagebrush Steppe
316	Miocene volcanics	clay	2935	Whitebark Pine Forest
281	Miocene volcanics	clay	1860	Jeffrey Pine Forest
Intermontane Plateaus				
Basin-and-Range, California				
diploid				
280	Pliocene or Pleistocene	sandy	1400	Sagebrush Steppe
Basin-and-Range, Nevada				
diploid				
288	Quaternary alluvium	clay	1980	Sagebrush Steppe
283	Jurassic volcanic?	clay	2135	Pinyon-Juniper Woodland
Columbia Plateau, Oregon				
tetraploid				
315	Pliocene gravels	talus	150	Sagebrush Steppe
Colorado Plateaus, Colorado				
diploid				
290	Eocene sedimentary	shale	1905	Pinyon-Juniper Woodland
286	Eocene sedimentary	shale	2950	Mountain Shrub
tetraploid				
287	Eocene sedimentary	loam	2145	Mountain Shrub
289	Cretaceous sandstone	sandy	2195	Pinyon-Juniper Woodland

TABLE 2. CONTINUED.

Popula- tion	Substrate	Soil	Eleva- tion (m)	Plant community
Rocky Mountains				
Colorado diploid				
292	Eocene volcanics	loam	2560	Ponderosa Pine Woodland
293	Precambrian granite	coarse sand	2740	Sagebrush Steppe
295	Precambrian granite	coarse sand	3025	Subalpine Forest
297	Pennsylvanian	sandy	2548	Subalpine Forest
tetraploid				
298	Cretaceous limestone	chalky fine	2432	Sagebrush Steppe
300	Eocene	clay	2500	Sagebrush Steppe
Wyoming hexaploid				
277	Quaternary	sandy	1950	Sagebrush Steppe
Wyoming Basin				
diploid				
305	Cretaceous sandstone	fine sand	1984	Sagebrush Steppe
hexaploid				
302	Precambrian	fine sand	2280	Sagebrush Steppe
Thompson Plateau, British Columbia				
diploid				
312	Eocene sedimentary	clay	442	Ponderosa Pine Forest
314	Precambrian metamorphic	clay	343	Ponderosa Pine Forest
tetraploid				
309	Pleistocene glacial	fine sand	868	Ponderosa Pine Forest
308	Cretaceous sedimentary	clay	460	Sagebrush Steppe

logically recent disturbance. In this view, diploids predominate on geologically older substrates because these substrates tend to occur in more mesic montane or riparian environments. Similarly, polyploids predominate on younger substrates because they occur in more arid environments on younger volcanic and alluvial substrates. The examples in Table 2 frequently contradict the climate hypoth-

esis. Compare, for example, Wyoming Basin populations 305 and 302. The diploid was in the Red Desert, the hexaploid in the Medicine Bow Mountains. Climatic explanations, it seems to me, too often have become a panchestron, an explain-all. Myriads of local climates exist in western North America, but reliable data describing them do not. Reliable data on rock and soil factors are easier to obtain, and can offer better explanations for distributions of ploidy levels in *C. douglasii*.

Substrate age hypotheses and other hypotheses need not be mutually exclusive. I suggested (Mooring 1980, p. 1317) that polyploid populations on geologically ancient, rather than recent, substrates could represent secondary adaptation to increasing aridity, particular soils, or both.

The observed correlation between ploidy level and age of substrate is a first step in explaining diploid-polyploid patterns in *Chaenactis douglasii*; it is a generalization that has predictive value. Much more often than not I have been able to predict the ploidy level of a population upon seeing it in the field for the first time.

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